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BREEDING HABITS OF THE ORTHOPTERA.

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CONTENTS.

INTRODUCTION.*

The Orthoptera are the most primitive insects according to Palæontological evidence. During the early Carboniferous period the insect fauna was composed entirely of the ancestors of this group, and during the latter part of the period the members of this stock far outnumbered that of any other order of insects. Fossil evidence proves that many of the primitive types are represented at the present by species that, in spite of the long intervening periods, have changed but little. New types have arisen, however, until the Orthoptera as they are now classified vary widely in their structure and habits, some being adapted to living in trees, others for life upon bushes and grass, others for cave and burrowing life and still others becoming social parasites, living in the nests of ants and obtaining their food from their hosts. As adaptations for the various modes of life have taken place certain phases of behaviour have kept pace and now present as many aspects as the varied structures and habits of the insects themselves.

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One of the most important of these special phases is that which attends the breeding activities and it is mainly with this aspect that this paper is concerned. It is impossible to describe the reproductive habits of all the Orthopteran forms as literature does not exist which would give the desired information. The activities of enough forms have been described, however, to permit a general comparison and a few generalities from the evidence thus presented.

The series of movements into which the entire process of reproduction may be divided will be considered separately and will be compared as units through the different families.

MOVEMENTS PRELIMINARY TO COPULATION. SEX DISCRIMINATION.

In some of the Orthoptera the movements preliminary to copulation are exceedingly simple. In others there is a complicated series of activities. Behaviour is the only criterion by which we may judge sex discrimination. It has been suggested that any movement which would indicate excitement after the two animals have come within sensing distance of each other might indicate recognition of sex. It must be borne in mind, however, that some of the Orthoptera are in a state of continual excitement during the breeding season, especially is this the case with males which have once copulated. In this state of excitement males will seize other males, members of other species or even a stick to which the abdomen of a female has been attached, so that it is not safe to base sex discrimination upon this one peculiarity of behaviour. On the other hand there is an entire lack of movements that would indicate excitement in some forms. Here the problem of sex discrimination is just as puzzling. No general statement in regard to sex discrimination would hold and each case must be considered separately.

The records of the sexual activities of the Blattidæ are very meager and in no case have their habits been described in detail. The sense of hearing is obviously not a factor as there are no organs for the reception of sound. Sight plays some part, for the male is described as running about the female trailing his abdomen and attempting to induce her to become quiet, even before they have come into contact with their antennæ. The senses of touch and of odor must play some part although no statement can be made as to their relative importance.

The Mantids have a very simple courting. When a male is introduced into a cage with a female during the breeding season he approaches her, raises his thorax, lowers his head and stands in this fixed position for some time. The female apparently pays no attention to him during this performance. After introducing himself in this manner he simply mounts the back of the female and copulation takes place. All the movements which are characteristic of the courting attitude occur before any contact of the antennæ or bodies has been established, so that touch and contact-odor seem to be secondary. There are no records of one male attempting to seize another, otherwise it might be contended that the sense of sight merely guided the two animals together and that the actual discrimination depended upon contact. Since discrimination is accomplished before any contact has been established, it seems that the most important factor is sight.

The Phasmids of which the walking sticks are common representatives, have very simple preliminary movements. They are mostly nocturnal in their habits and copulation takes place at night or in very dim light. No contact seems to be necessary and if sight furnishes the male with any information concerning the sex of his mate there is no excitement to indicate the fact. Without any preliminary movements whatever, the male mounts and copulates. Stockard ('08) describes some interesting experiments in which he proves that no complex combination of the senses are required for accomplishing sex discrimination. He cut off the end of the female's abdomen and fixed it to a stick which had been furnished with wire legs and it was found that the male copulated with this piece of abdomen quite as readily as with the normal female. Stockard also maintains that the experiment proves that no response on the part of the female is necessary to induce the male to copulate.

The Acrididæ or short-horned grasshoppers include a great number of genera and species which show a wide variation in their structure and a lesser degree of variation in their behaviour. A more or less constant type of behaviour preliminary to copulation, however, makes it appear that sex discrimination is accomplished in the same manner for the entire group. One factor in the ordinary behaviour of the Acrididæ which may be of some significance for mating seems to have been entirely disregarded. Most of the insects have organs for the reception

of sound. During flight a dry crackling sound is made by the wings and there is a brilliant display of color. It seems reasonable that organs for making and receiving sounds which play so important part in the sexual activities of the Locustidæ and of the Gryllidæ should not be without a similar function here. The usual movements of the male of the Acrididæ consist of a few convulsive jerks of the body as he sights the female, followed by a creeping toward her until he is within springing distance. Some investigators have stated that the male will spring upon the female from a distance of three or four feet. In the Tettigidæ (grouse locusts) this process is modified somewhat. The male does not spring but, creeping toward the female, he makes a rush and mounts from the side. It is not uncommon for males of one species to spring upon other males or for males to mate with the females of an entirely different species. Species differing as widely as Hippiscus rugosum and Melanoplus femur-rubrum have been found in copulation. These facts suggest that sex discrimination and even species discrimination is of a low order in this group. Sight and possibly sound furnish the stimulus for the beginning of the preliminary movements, but an actual body contact seems to be necessary for a final discrimination of sex.

The Locustidæ with their great variety of habits and structure furnish some of the most interesting variations in their preliminary movements. Some are nocturnal; some are diurnal; some are winged; some are not; some have very complex movements attending their copulation, some mate very simply. Some forms like the katy-did have membraneous organs in the wings for producing sounds. The shrilling of the male as he attempts to call the female to him is one of the most common sounds of the late summer nights. When a female has been induced to approach the male stops shrilling and the two indulge in a preliminary fencing with the antennæ. Here we may assume that the sense of hearing was the first factor used in bringing the two sexes together. The sense of sight evidently does not play an important part here. In the Mormon Cricket (Anabrus simplex), however, sight is apparently the most important factor while hearing plays a secondary part. Anabrus is diurnal and congregates in great numbers on the prairie during the breeding season. The preliminary movements have not been observed but since the only sound uttered is a faint

squeak, hearing does not seem to be so important. Among the Locustidæ are found species which are not only wingless but have no means of making sounds. These are nocturnal and representative. Ceuthophilus stygius, a species living in the caves of Indiana, has eyes that have become somewhat rudimentary. Since it breeds "far back beyond the reach of any rays of light," (Blatchley, '02) and is devoid of hearing organs, the only senses left to it for its sexual activities are those of smell and touch. In Ceuthophilus latens the writer found that although the eyes are well developed they are not used in the sexual activities of the animal, sex discrimination depending upon contact and possibly odor. In the Locustidæ then, sex discrimination is accomplished in some cases by contact (perhaps "contact odor") alone, in others by contact and sight and in still others by contact, sight and hearing.

The true crickets, or Gryllidæ, present nearly as wide a variation in their preliminary movements as do the Locustidæ. Chirping is a common habit with both the nocturnal and the diurnal crickets and is without doubt a sex call. In some of the nocturnal forms the sense of sight is evidently used but little and the sense of hearing is relatively important. The field and ground crickets have similar copulating habits. After a female has approached in response to the call of the male the usual fencing with the antennæ ensues and then the male, turning around and raising his wings, invites the female to mount. The tree cricket (Oecanthus) has been much observed and its habits described in detail. The female becomes greatly excited upon hearing the call of the male and in going to him in response to the call seems to be directed by the sound. (Jensen, 1908.)

The mole cricket (subfamily Gryllotalpinæ) breeds underground in tunnels which it constructs. (Baumgartner, '10.) Although it is obliged to carry on all its mating activities in the dark, the loss of opportunity to use the sense of sight is compensated for by the presence of a chirping organ in the female. She answers the call of the male until they have come into contact, and the problem of their uniting is simplified.

Sex recognition in the Gryllidæ is accomplished in all cases with the aid of the sense of hearing and in some without the possibility of aid by sight. How much of a part actual contact plays it is difficult to say, but the movements that would indicate a sexual excitement frequently are begun with the aid

of no other sense than that of hearing. In all the families previously mentioned, except the Locustidæ, the female is a passive party in the process of copulation. In the Locustidæ she plays an active part in coming to the male in answer to his call. In the Gryllidæ she must take a still more active part and actually mount the back of the male before copulation can take place. It is a far cry from the Phasmid in which the female is so passive that the male will copulate with her abdomen which has been fastened to a stick and the female of the cricket which must not only find the male but even mount his back. Little power of discrimination would be conceded to the female of the Phasmid while in the cricket it appears that the female must have a highly developed discrimination. Since in the Phasmid it would be simply lost motion for the male to go through a series of complicated movements before such an unresponsive female, no such movements have been developed and copulation is very simple. In the cricket, on the other hand, the male must first make his whereabouts known and must then demonstrate his sex before the female will mount. Sex discrimination in the female and complication of preliminary movements have developed hand in hand.

COPULATION.

Under this topic will be discussed mainly the relative position of the bodies of male and female during copulation, the duration of copulation and the method of transfer of spermatozoa.

Since in the Cockroach the process is so rapid that the details cannot be followed, it can only be said that the male shoves his body under that of the female and accomplishes the transfer of spermatozoa in a few seconds.

The male Mantid simply mounts and copulates sometimes retaining his position for as long as seven hours. The spermatozoa are transferred directly to the oviducts and if there is any spermatophore present it is not visible externally. The habit of cannibalism is highly developed among the Mantids. If a pair is kept in captivity during their copulation, the female will invariably devour the male, although he is usually given a respite of an hour or so. Not infrequently, however, the male is devoured during the actual process of copulation. This has been observed in nature as well as in animals kept in captivity. Fabre thinks that this habit is a relic of the Carboniferous

period when the Mantid was one of the few insects and when there would be a natural dearth of food. Then the male was habitually devoured as the most available source of food. A female will copulate with as many as seven males in a single season.

Copulation is as simple in the Phasmids as it is in the Mantids. The male mounts the back of the female and curling his abdomen under and to one side of that of the female he effects the union. Copulation lasts for several hours.

The method of copulation in the Acrididæ is fairly constant. The male, after assuming his position upon the back of the female, bends his abdomen to one side and under that of the female and copulates. Copulation between a single pair lasts for hours and sometimes as long as two days. There is no spermatophore, the spermatozoa being transferred directly to the oviducts by a bifurcated intromittent organ.

In spite of the great variety exhibited in the structure and habits of the Locustidæ there is a fairly constant mode of copulation. It may be termed an "end to end" position. In some cases both of the animals are in a vertical position on grass stems; sometimes the male is curled beneath the female, or even standing on his head. In the case of Ceuthophilus both animals stand upright, facing in opposite directions, while the end of the abdomen of the male is inverted and grasps that of the female by the subgenital plate. This may be taken as a typical position while the others are variations necessitated by circumstances. The mating pair may be located upon parallel or upon diverging stems, upon the ground in a horizontal position or the female may be running about dragging the male in any position. Copulation is of short duration, generally lasting a few minutes and the spermatozoa are transferred by means of spermatophore. This spermatophore when visible externally appears as a lobed membranous sac which is translucent at first but becomes opaque after a short exposure to the air. It appears shortly after the union of the two animals and is quickly transferred by the male to the vulva of the female where it hangs until the contained spermatozoa have made their way into the oviducts.

The relative position of the bodies of the male and the female is constant throughout the entire group of the Gryllidæ.

The female mounts the back of the male and a spermatophore is fixed to her vulva by the male. The transfer of the spermatophore takes only a few minutes but the animals remain in their positions for a short time before separating. As soon as she is free from the male the female begins to gnaw at the spermatophore and it seems that nature has provided a special organ for keeping her attention diverted long enough to allow the spermatozoa to enter the oviducts. At the base of the male's wing is located a gland which exudes a viscous liquid which is evidently very palatable to the female for she gnaws at it constantly during copulation, and is kept occupied for some time after the spermatophore has been transferred.

From the evidence drawn it is safe to say that each family of the Orthoptera has a fairly constant mode of copulation, and that insofar as any specialization is shown it has its greatest development in the Locustidæ and in the Gryllidæ.

OVIPOSITION.

The process of egg-laying is very simple in some of the Orthoptera and complex in others.

The oviposition of the Cockroach may be considered a very specialized type. Sixteen eggs are deposited by the female in a horny capsule which is secreted inside of her body. Some of the Cockroaches deposit this capsule as soon as it is formed, while others carry it about, partially protruding from the body, until the young are nearly ready to hatch. Then it is deposited in some convenient crevice. The capsule is a brown, horny structure which is in the shape of a flattened oval measuring about 12 mm. in length and 6 mm. in width. It is furrowed by a series of fine annulations, and provided with a lateral notched carina. The eggs are arranged in two symmetrical rows of eight each.

Egg-laying among the Mantids is a very complicated process. A single female lays a great many eggs, all of which are deposited at one time and enclosed in a fibrous öotheca. The öotheca is attached to a twig, a stone, or to any suitable object that may be at hand. In making the ootheca a small amount of a viscous liquid is extruded from the oviducts and the genital plates immediately begin whipping the liquid into a foam. More liquid is extruded and the whipping continues.

From time to time the abdomen is buried deep in the mass, and it is supposed that actual egg-laying occurs at this time. The time required for completion of the egg case is about two hours. The öotheca as it is finally left by the female is a rough, oval structure composed in its interior of horny material which gives place near the surface to an alveolar structure. The outer covering resembles tough silk in its consistency. The eggs are arranged in regular tiers in the center of the case. The entire structure is an admirable one for resisting the rigors of the weather as well as the attacks of insects and of parasites.

The Phasmids have a type of egg-laying that appears to be most simple. The eggs are simply discharged at random and fall to the ground. The fact that a fairly well developed ovipositor still persists in the Phasmids which practice this random method of oviposition seems to indicate that this method of deposit is a recently acquired one.

When the female of the Acrididæ is ready to lay her eggs, she brings forward the end of her abdomen, and inserting it into the ground at a sharp angle to the axis of the body, she works the valves of the ovipositor and shoves with the abdomen until the entire posterior end of the body is buried in the ground. Having accomplished this, she fills the cavity which she has made with eggs arranged in oblique columns and at the same time she exudes a viscous liquid which fills the hole and binds the eggs together. Some of the grouse locusts on account of their small bodies and short abdomens can construct only shallow burrows. Such animals frequently lay in moss where the eggs are protected by their resemblance to seeds found there.

The Locustidæ and the Gryllidæ present a wide variation in their manner of egg-depositing. The Katydids live mainly on bushes and trees and deposit their eggs there. In some instances the eggs are glued to the side of a twig and in others they are stuck to the edge of a leaf, or even enclosed in the end of a leaf which has been split for this purpose. When a female is ready to deposit her eggs, she roughens the surface of the twig and removes any buds or other projections. Then bringing forward the end of her scimiter-shaped ovipositor she guides it into the correct position by means of her palpi and jaws and then emits a glue-like liquid which adheres to the twig. The egg then appears shiny black at first, but turns gray later and is glued fast so that it lies at a slight angle to the twig.

The process is repeated, each egg overlapping the preceding one, until a row has been deposited. The eggs are oval but are very much flattened, resembling hemp seeds in shape. The cone-headed grasshoppers have blade-like ovipositors of different shapes, some being short and curved, others very long, straight and pointed. These serve for inserting the eggs between the leaves and stems of grass upon which the insects live. Ground dwelling Locustidæ such as Anabrus and Ceuthophilus, have their ovipositors modified for piercing the ground. That of Ceuthophilus is slender but strong and is equipped with five teeth at its apex.

The ground and field crickets lay their eggs, singly or in groups of from two to five, in the ground. The long needle-like ovipositor is admirably adapted for thrusting into the ground. The tree crickets (Oecanthinæ) have retained the long, needle-like ovipositor but have modified its use to suit their changed habitat. Stems containing pith are usually selected for egg receptors, raspberry stems being most favorable. The female begins operations by biting the twig and roughening it so that the ovipositor may gain an entrance. The ovipositor is then brought up, placed upon the roughened spot and by vigorous working of the blades and thrusting with the abdomen, the twig is pierced to the depth desired. The egg is deposited and crowded tightly into the hole by the ovipositor after which it is covered and left. The same process is repeated until the twig contains a long row of eggs in the pith almost perpendicular to the long axis of the twig.

The mole crickets do not have a well developed ovipositor. The eggs are deposited by simply dumping them in a heap in one of the subterranean chambers. Contrary to the habits of the other crickets, however, the eggs are watched and cared for until they hatch.

On the whole the Acrididæ may be considered to have the most generalized type of egg-laying. The Blattidæ and the Mantids have been specialized in the direction of highly developed egg-cases while the Locustidæ and the Gryllidæ have become specialized in the habit of laying the eggs singly or in small groups, each single egg or group in its own prepared cavity.

SPECIALIZED AND SIMPLE TYPES OF REPRODUCTIVE BEHAVIOUR.

In considering the different aspects of the reproductive behaviour, (preliminary movements, oviposition, etc.), the Acrididæ appear to be the least specialized. The Cockroaches and the Mantids are specialized in the habit of constructing egg capsules and cocoons. The Locustidæ and the Gryllidæ have developed their preliminary movements to a great extent and also have a specialized type of oviposition, but different from the Cockroaches and the Mantids. The Acrididæ seem to be specialized in neither regard and occupy a somewhat intermediate position as regards egg-laying and preliminary movements.

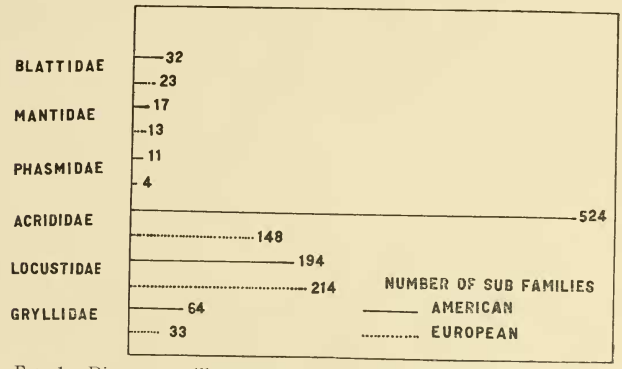

FIG. 1. Diagram to illustrate effect of specialization upon the number of sub-families in each group of the Orthoptera.

It is a well known fact that specialization in any habit, especially in breeding habits confines the animal to a more limited field and lessens its chances for adjusting itself to changes in environment. Consequently the animal which has the more general habits can occupy the larger general field and so have a larger representation. Figure 1 represents the total number of subfamilies in each group of the Orthoptera in the Holoarctic realm. The Acrididæ far outnumber the other groups. Locally one subfamily may predominate as it finds conditions favorable to its mode of specialization; but in general, non-specialized conditions will prevail, and it is the type of animal which has the least degree of specialization that

will have the largest representation. It is possible that conditions have arisen in Europe that have been temporarily very favorable to the type of specialization of the Locustidæ, causing them to attain to greater diversity than the Acrididæ in that region or the Locustidæ in America.

The Phasmids and the Mantids have their greatest development in the tropics. Consequently they are poorly represented in the more generalized temperate climates of Europe and of the United States.

AN ATTEMPT TO CLASSIFY THE ORTHOPTERA ACCORDING TO THEIR REPRODUCTIVE BEHAVIOUR.

Figures 2, 3 and 4 are schemes based upon one or two factors of reproduction while Figure 5 represents a classification based upon all the factors collectively.

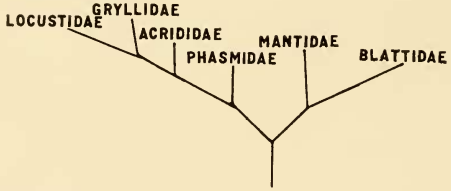

*Fig. 2. Classification based upon specialization of the ovipositor, Rudimentary ovipositor in Blattidæ and Mantidæ, intermediate development in Phasmidæ and Acrididæ, maximum development in Gryllidæ and Locustidæ.

In Figure 2 the classification is based upon the amount and direction of specialization of the ovipositor. The first division separates the Mantids and the Cockroaches from the others because of the lack of an external ovipositor. In both forms the ovipositor is relatively undeveloped. The Phasmids are included with the Acrididæ, the Gryllidæ and the Locustidæ because they have a fairly well developed ovipositor although it apparently is not used. The Acrididæ are separated from the Locustidæ and the Gryllidæ because of their relatively short and undeveloped ovipositor. The Locustidæ and the Gryllidæ as a whole have highly specialized ovipositors although some have suffered an almost complete loss of the organ due to their change of life. Reading from right to left we have a more or

*In Figs. 2, 3, 4 and 5 direction and extremes of factors used in classification are indicated in horizontal plane.

less regular sequence; first, the non-development of an external ovipositor; second, an ovipositor developed but nonfunctional; third, a comparatively unspecialized ovipositor and lastly, a highly specialized and functional ovipositor.

The classification in Figure 3 is based upon the presence of a definite egg-capsule or the approach to it in those forms which do not possess it. As in Figure 2 the Mantids and Blattids stand apart from the other forms being divided from the other forms because of their possession of an egg capsule or öotheca. The Locustidæ and the Gryllidæ again occur at the other extreme, because they lay their eggs singly or in masses of only two or three. Again the Acrididæ occupy an intermediate position because they resemble the Blattidæ and the Mantidæ in

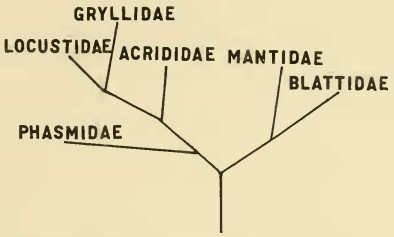

FIG. 3. Classification based upon the occurrence of an egg capsule. Mantidæ and Blattidæ having a definite ootheca are placed by themselves. Gryllidæ and Locustidæ laying eggs singly are placed at the opposite extreme. Acrididæ, laying eggs in compact mass are placed between. Phasmidæ are placed near Acrididæ because eggs are all discharged at once. Since they have no approach to an ootheca they are inclined to the left extreme.

laying their eggs all at once but in not having a definite egg capsule. The position of the Phasmids in this classification is doubtful. The fact that they choose no special place for depositing their eggs and that they deposit them in a very loose manner, indicates a rather low degree of specialization. They have been placed near the Locustidæ and the Gryllidæ because they resemble these families in depositing their eggs singly.

In Figure 4 three factors are considered in the classification of one of the stems established in Figures 2 and 3. These factors are the presence or the absence of a spermatophore, the relative position of the bodies during copulation and the duration of copulation. The three factors are intimately associated.

Long duration of copulation, the absence of a spermatophore and the superposition of the body of the male during copulation divides the Phasmids and the Acrididæ at once from the Locustidæ and the Gryllidæ. Minor peculiarities in these factors permit a division between the Acrididæ and the Phasmids. The Locustidæ and the Gryllidæ have a short duration of copulation, and a spermatophore which is usually visible. The Locustidæ and the Gryllidæ may be divided upon the ground that there is a superposition of the body of the female in the Gryllidæ and an "end to end" position of the bodies in the Locustidæ. The mole crickets may be divided from the other Gryllidæ because of their peculiar modification of the usual body position.

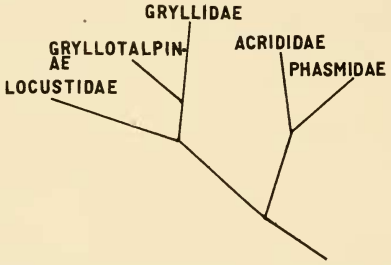

Fig. 4. Classification based upon the development of spermatophores in those forms showing an inclination toward this structure. Acrididæ and Phasmidæ, having sperm masses resembling spermatophores but not enclosed in a membrane, are placed at one extreme. Gryllidæ have definite spermatophore, but highest development is reached in Locustidæ, which are placed on the left extreme.

An attempt is made in Figure 5 to summarize the factors that have been named as well as some additional ones. The main division is made because of the following facts: The Blattidæ and the Mantidæ have a definite egg capsule or ootheca; they have no development of an external ovipositor for inserting eggs into the ground or into twigs and they neither produce sounds nor have organs for the reception of sounds. The other groups are united because they possess ovipositors, because they have organs for producing and receiving sound and because they do not lay their eggs in a capsule. The position of the Phasmids is doubtful but a consideration of all their breeding habits will place them in the position shown, nearer to

the Acrididæ than to the Mantidæ. The Blattidæ and the Mantidæ may be divided because of the peculiar manner in which each constructs its egg case. A further subdivision of the Blattidæ is made to include the myrmecophilous forms. The stem including the Acrididæ and the Phasmidæ is separated off because of the following factors: These two forms have a relatively poor development of the ovipositor, and a superposition of the body of the male during copulation. Eggs are laid all at one time, sounds are produced which consist of a crackling of the wings, hearing organs are present and are located in the base of the abdomen. In the Locustidæ and the Crickets on the other

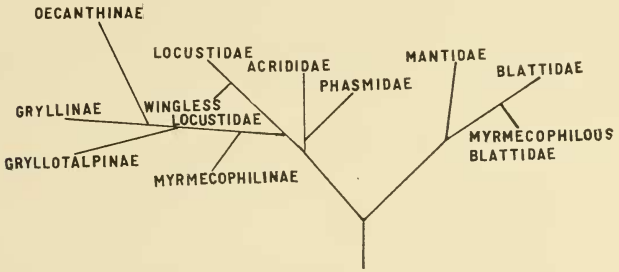

*Fig. 5. Classification based upon summary of factors in three preceding schemes. Right extreme indicates presence of definite ootheca, long duration of copulation, superposition of body of male during copulation (in Mantidæ), absence of organs for production and reception of sounds and the absence of an ovipositor. The left extreme indicates a complication of movements prior to copulation, absence of an ootheca, eggs laid singly, superposition of body of female during copulation, presence of stridulating organs and organs for the reception of sound. Forms placed in various intermediate positions show a lesser degree of specialization.

hand the ovipositor is well developed and specialized, the bodies are found in various positions during the copulation but there is no superposition of the body of the male, eggs are laid singly or in masses of two or three, sounds produced consist of chirps, and the organs for the reception of sounds are located in the anterior tibia. The Acrididæ and the Phasmids are separable because of differences already mentioned. A subdivision of the Locustidæ is made because some forms have suffered a degen-

*Horizontal plane indicates general direction and extremes of summary of factors and processes used in classification. Lines inclined upward indicate development and specialization of organs and processes, while lines inclined downward indicate degeneration or loss of organs. Extent of lines indicates to-some degree the amount of development or degeneration.

eration of those very factors which mark them off from the other groups. The forms that have entirely lost their wings have lost their capacity for producing sounds. In Ceuthophilus the organs for the reception of sound have also been lost. The factors by which we may divide the Locustidæ from the Crickets are not so conspicuous. The modification which the ovipositor has undergone in each group will suffice for their division. The relative position of the bodies of the male and of the female during copulation is another factor which may divide them. The diversity found among the crickets makes further subdivision possible in that group. The activities of the field crickets may be regarded as the most typical for the Gryllidæ. The tree crickets (Oecanthinæ) being specialized in their manner of ovipositing are given a separate standing. The mole crickets, because of the absence of the ovipositor, the changed manner of depositing the eggs, and because of the development of a chirping organ in the female, have been placed in a separate division. Little is known of the reproductive habits of the myrmecophilous crickets and Blattids. In European forms only the females have been discovered. Both males and females, however, have been found in an American form by Wheeler. (Wheeler, 1900.) The reproductive activity must differ somewhat from the typical mode. Consequently they are given a separate rating as indicated in the diagram.

Having made such a classification it must be admitted that the behaviour of each group depends to some extent upon structural characteristics so that the classification really rests upon morphological characters, the basis adopted by taxonomists for classification. The structural characteristics have been used, however, only when they have some intimate connection with the reproductive behaviour.

A glance at the ancestral tree of the Orthoptera, (Fig. 6), will show some striking resemblances to the classification based upon the reproductive behaviour (Fig. 5). The fossil evidence bearing upon the ancestry of the Orthoptera has been thoroughly worked out by Anton Handlirsch ('08), and a genealogical tree constructed to show the relations of the different families. Figure 6 represents the essentials of his scheme. The Blattidæ and the Mantidæ are entirely divided off as early as the Carboniferous period. The stock from which the other groups have arisen was divided into two rather definite

divisions, one including the Phasmids and the Acrididæ with some others that are not being considered here for want of information concerning their habits, and the other the Locustidæ and the crickets. The Gryllotalpinæ have arisen in comparatively recent times from the typical stock of the Gryllidæ.

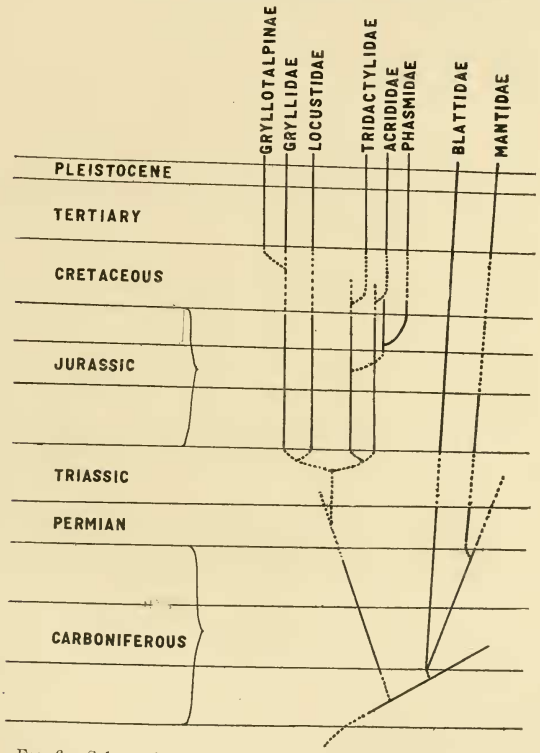

FIG. 6. Scheme indicating the phylogeny of the Orthoptera.

A comparative study of Figures 5 and 6 suggests that the agreement between the diagrams is not a mere coincidence. From a common ancestral stock specialized types have arisen, some persisting and others perishing. We may assume that

the variations arose, first, because the animals were subjected to a new environment and the necessary modifications in the behaviour caused modifications in structure, or that variations in structure arose by orthogenesis and the animals were called upon to find a suitable environment or perish. The latter assumption seems to be the most reasonable. The agreement between the two figures also suggests that the more fundamental modifications in structure and in behaviour have been fairly constant since their origin.

SUMMARY.

1. Movements preliminary to copulation are fairly constant for each group of the Orthoptera and vary from very simple (Mantidæ, Phasmidæ and Acrididæ) to complex (Blattidæ, Gryllidæ and Locustidæ).

2. There is a sex discrimination in the males of all forms. The female plays an aggressive part and displays a discrimination of sex in some groups while in others she is absolutely passive.

3. There is a typical mode of copulation for each family of the Orthoptera. In the Mantidæ, the Phasmidæ and the Acrididæ there is a superposition of the body of the male. In the Blattidæ and the Gryllidæ there is a superposition of the body of the female. In the Locustidæ there is an "end to end" copulation.

4. Families represented by the least number of subfamilies are highly specialized while those represented by the largest number of subfamilies have a generalized type of reproductive behaviour.

5. A comparison between a classification based upon the reproductive behaviour and one based upon pæleontological evidence shows a striking agreement and suggests that the different types of reproductive behaviour have been fairly constant since their origin.

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